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Target Patterns in Reaction–Diffusion Systems

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We consider the general reaction–diffusion system $A_t = F(A) + \epsilon D_M \nabla^2 A + \epsilon g(\vec{x}, A)$, $0 < \epsilon \ll 1$, where the small term $\epsilon g(\vec{x}, A)$ represents the effects of localized impurities. We assume that the system $A_t = F(A)$ has a stable time-periodic solution. Then we construct stable target pattern solutions of the full system. For typical initial conditions we find that these target patterns will arise only if $g(\vec{x}, A) \not\equiv 0$. Finally, we determine how target patterns interact and show that higher frequency target patterns eventually engulf neighboring lower frequency target patterns.

1. Introduction

In some chemical and biological systems confined to two spatial dimensions, target patterns are commonly observed: concentric circular concentration waves which expand outward with new waves being generated at the center. For example, Belousov–Zhabotinski (B–Z) reactions [1–4] exhibit target patterns, as do fields of aggregating *D. discoideum* [5–8]. (See Fig. 1.)

Target patterns have been investigated previously [9–15]. Here we consider the general system

$$A_t = F(A) + \epsilon D_M \nabla^2 A + \epsilon g(\vec{x}, A), \qquad 0 < \epsilon \ll 1. \qquad (1.1)$$

In (1.1) the diffusion term is small because we have chosen to look for solutions which vary on long spatial scales. We have done this since diffusion tends to make A spatially uniform. Also, (1.1) is spatially inhomogeneous due to the small term $\epsilon g(\vec{x}, A)$. For the B–Z reaction, this term can arise from particle contaminants and other impurities [3]. For fields of *D. discoideum*, this term arises from the different starvation states of the individual amoebas [6].

We will construct formally stable target pattern solutions of (1.1), first for the case $g(\vec{x}, A) \equiv 0$ and then for the general case $g(\vec{x}, A) \not\equiv 0$. We will find
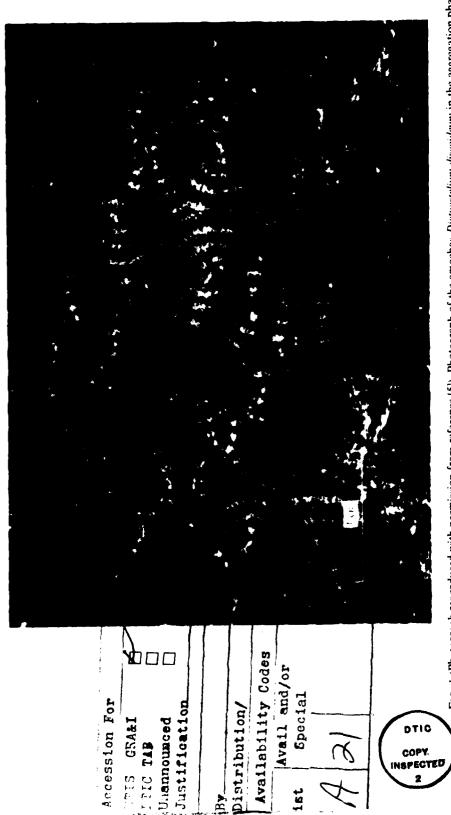
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FIG. 1 (Photograph reproduced with permission from reference [5]). Photograph of the amoebas *Dictyostelium discoideum* in the aggregation phase. The light bands are bands of moving cells. Both target patterns and spiral waves are present.

that the target patterns for $g(\vec{x}, A) \equiv 0$ occur only for special initial conditions. However, for $g(\vec{x}, A) \not\equiv 0$ they arise even if the system is initially well stirred.

This matches the experimental observations of the B–Z reaction in [3]. There it is reported that there are small particles at the centers of most target patterns, and that filtration of the chemicals to remove impurities eliminates nearly all of the target patterns.

We also determine how target patterns interact. We find that higher frequency target patterns engulf nearby lower frequency patterns. This matches the observations in [1].

2. The Governing Equation

We assume that at $\epsilon = 0$, system (1.1) has a stable time-periodic solution $A(t, \vec{x}) = B(t) \equiv B(t + P)$ with period P. We now use two-timing to solve (1.1). We let $T = \epsilon t$, we expand A as

$$A(\epsilon, t, \vec{x}) = A^0(t, T, \vec{x}) + \epsilon A^1(t, T, \vec{x}) + \cdots, \qquad (2.1)$$

and we require $A^1, A^2, \ldots$, to be bounded in t. Substituting (2.1) into (1.1) we find

$$A^0_t - F(A^0) = 0, \qquad (2.2)$$

$$A^1_t - F_A(A^0)A^1 = -A^0_T + D_M \nabla^2 A^0 + g(\vec{x}, A^0), \qquad (2.3)$$

$$\vdots \qquad \vdots$$

Here the matrix $F_A(A^0)$ is the derivative of $F(A)$ with respect to A.
  The solution of (2.2) of interest is

$$A^0 = B(t + \psi(T, \vec{x})), \qquad (2.4)$$

where the function $\psi(T, \vec{x})$ is undetermined at this stage. Substituting (2.4) into (2.3), we obtain

$$A^1_t - F_A(B)A^1 = -B'\psi_T + D_M B' \nabla^2 \psi + D_M B'' \vec{\nabla}\psi \cdot \vec{\nabla}\psi + g(\vec{x}, B), \qquad (2.5)$$

where the argument of B, B', and B'' is $t + \psi(T, \vec{x})$.
  Now the equation

$$u_t - F_A(B(t + \psi))u = 0 \qquad (2.6)$$

has a periodic solution $\mathbf{u} = \mathbf{B}'(t + \psi)$. To ensure that $\mathbf{A}^0 = \mathbf{B}(t + \psi)$ is a stable solution of (2.2), we assume that all solutions of (2.6) which are linearly independent of $\mathbf{B}'(t + \psi)$ decay exponentially. Under these conditions there is a unique row vector $\mathbf{z}^T(t + \psi)$ which satisfies

$$\mathbf{z}_t^T + \mathbf{z}^T F_A(\mathbf{B}[t + \psi]) = \mathbf{0}^T, \qquad \mathbf{z}^T(t + \psi)\mathbf{B}'(t + \psi) = 1, \qquad \text{for all } t,$$
(2.7)

and is periodic with period P. Moreover, the solution $\mathbf{A}^1(t, T, \vec{x})$ of (2.5) is bounded in t if and only if

$$\int_0^P \mathbf{z}^T\left[-\mathbf{B}'\psi_T + D_M\mathbf{B}'\nabla^2\psi + D_M\mathbf{B}''\vec{\nabla}\psi \cdot \vec{\nabla}\psi + \mathbf{g}(\vec{x},\mathbf{B})\right]ds = 0,$$
(2.8)

where the argument of $\mathbf{z}^T$ and $\mathbf{B}$ is $s + \psi(T, \vec{x})$. Using periodicity, we rewrite (2.8) as

$$\psi_T = D(\nabla^2\psi + \Gamma\vec{\nabla}\psi \cdot \vec{\nabla}\psi) + \alpha(\vec{x}),$$
(2.9)

where the constants D, Γ and the function $\alpha(\vec{x})$ are

$$D \equiv \int_0^P \mathbf{z}^T(s)D_M\mathbf{B}'(s)\,ds/P, \qquad D\Gamma \equiv \int_0^P \mathbf{z}^T(s)D_M\mathbf{B}''(s)\,ds/P,$$

$$\alpha(\vec{x}) \equiv \int_0^P \mathbf{z}^T(s)\mathbf{g}(\vec{x},\mathbf{B}(s))\,ds/P.$$
(2.10)

In summary,

$$\mathbf{A}(t, \vec{x}) = \mathbf{B}(t + \psi(T, \vec{x})) + 0(\epsilon),$$
(2.11)

where ψ evolves on the long time scale $T = \epsilon t$ according to (2.9). Equation (2.9) is the key equation that describes how target patterns evolve and interact. The derivation of (2.9) from (1.1) is very similar to a result of John Neu [16].

To interpret the $\alpha(\vec{x})$ term in (2.9), consider (1.1) with the diffusion matrix D_M set to 0. Since $\epsilon \ll 1$, at each spatial position $\vec{x}$ there must be a stable time-periodic solution near $\mathbf{B}(t)$. To find this solution, we note that $D_M = 0$ in (2.10) implies that $D = 0$, so (2.9) shows that $\psi = \alpha(\vec{x})T$. Substituting this into (2.11), we find that $\mathbf{A} = \mathbf{B}(t[1 + \epsilon\alpha(\vec{x}) + \cdots]) + 0(\epsilon)$. Thus the $\alpha(\vec{x})$ term in (2.9) represents the local first-order frequency shift due to the inhomogeneous term $\epsilon\mathbf{g}(\vec{x},\mathbf{A})$.

3. SPATIALLY HOMOGENEOUS SYSTEMS

Here we consider systems with $g(\vec{x}, \mathbf{A}) \equiv \mathbf{0}$. Then (2.10) shows that $\alpha(\vec{x}) \equiv 0$, so (2.9) becomes

$$\psi_T = D[\nabla^2 \psi + \Gamma \vec{\nabla} \psi \cdot \vec{\nabla} \psi]. \tag{3.1}$$

To solve (3.1) we apply the Cole–Hopf transformation

$$Z = e^{\Gamma \psi}, \tag{3.2}$$

finding

$$Z_T = D \nabla^2 Z. \tag{3.3}$$

The initial value problem for (3.1) can be solved by solving the initial value problem for (3.3). Thus, in n space dimensions

$$\psi(T, \vec{x}) = \Gamma^{-1} \log \left\{ (4\pi DT)^{-n/2} \int \exp[\Gamma \psi(0, \vec{y}) \right.$$

$$\left. - (\vec{x} - \vec{y}) \cdot (\vec{x} - \vec{y})/4DT] \, dy \right\}. \tag{3.4}$$

Now (3.4) shows that if $\psi(0, \vec{x})$ is bounded, then $\psi(T, \vec{x})$ goes to a constant as T becomes large. Thus when $g(\vec{x}, \mathbf{A}) \equiv \mathbf{0}$, no target patterns evolve for bounded initial conditions.

Next, we construct stable target pattern solutions of (1.1) with $g(\vec{x}, \mathbf{A}) \equiv \mathbf{0}$. These solutions must have $\psi(0, \vec{x})$ unbounded, and so they may be of mathematical interest only.

By solving (3.3) and using (3.2), we find that (3.1) has the solutions

$$\psi(T, \vec{x}) = \omega T/\Gamma + \Gamma^{-1} \log I_0(\sqrt{\omega/D}\, r), \tag{3.5}$$

in two dimensions and

$$\psi(T, \vec{x}) = \omega T/\Gamma + \Gamma^{-1} \log\{r^{-1} \sinh \sqrt{\omega/D}\, r\}, \tag{3.6}$$

in three. Here $r \equiv |\vec{x}|$, I_0 is the zero-order modified Bessel function, and ω is any positive constant. Moreover (3.4) shows that the solutions in (3.5) and (3.6) are stable to all bounded initial perturbations.

Equations (2.11) and (3.5) yield target pattern solutions in two dimensions. Similarly, (2.11) and (3.6) yield time-periodic, spherically symmetric solutions in three dimensions. When $r \gg 1$, both (2.11), (3.5) and (2.11),

(3.6) reduce to

$$A(t, \vec{x}) \sim B\left([1 + \epsilon\omega/\Gamma]t + \sqrt{\omega/D}\,r/\Gamma + \cdots\right) + 0(\epsilon). \qquad (3.7)$$

Since $\epsilon \ll 1$, these waves are ingoing if $\Gamma > 0$ and outgoing if $\Gamma < 0$.

Target patterns are observed in the B–Z reaction and in *D. discoideum*, even if the systems are well stirred initially so that $\psi(0, \vec{x})$ is nearly constant. In the next section we show that the observed target patterns can be explained if the inhomogeneous term $g(\vec{x}, A)$ is not identically zero.

4. SPATIALLY INHOMOGENEOUS SYSTEMS

Here we consider the inhomogeneous case, where $g(\vec{x}, A) \not\equiv 0$ in (1.1) and hence $\alpha(\vec{x}) \not\equiv 0$ in (2.9). Specifically, we assume that $\alpha(\vec{x})$ is smooth and that $\int \Gamma\alpha(\vec{x})\,dx > 0$, where the integration is over all space. For mathematical clarity, we also temporarily assume that $\alpha(\vec{x}) = 0$ for all $|\vec{x} - \vec{x}_0| > R$, for some fixed $\vec{x}_0$ and R. With these restrictions on $\alpha(\vec{x})$, we will now solve (2.9) for bounded initial conditions $\psi(0, \vec{x})$. We will find that the solution $\psi(T, \vec{x})$, together with (2.11), will yield a single target pattern centered near $\vec{x} = \vec{x}_0$. This target pattern will depend only on $\alpha(\vec{x})$, D, and Γ, and will be independent of the initial condition $\psi(0, \vec{x})$.

First, we apply the Cole–Hopf transformation (3.2) to (2.9), finding

$$Z_T = D\nabla^2 Z + \Gamma\alpha(\vec{x})Z, \qquad Z(0, \vec{x}) = e^{\Gamma\psi(0, \vec{x})}. \qquad (4.1)$$

Next, we separate variables $Z(T, \vec{x}) = e^{\omega T}\Phi(\vec{x})$, obtaining the eigenvalue problem

$$D\nabla^2\Phi + \Gamma\alpha(\vec{x})\Phi = \omega\Phi, \qquad \Phi(\vec{x}) \text{ bounded.} \qquad (4.2)$$

With the restrictions placed on $\alpha(\vec{x})$, it is known [17, 18] that in two dimensions there are a finite number $m \geq 1$ of discrete real eigenfunctions $\Phi_1(\vec{x}), \Phi_2(\vec{x}), \ldots, \Phi_m(\vec{x})$. Their eigenvalues $\omega_1, \ldots, \omega_m$ satisfy

$$\omega_1 > \omega_2 \geq \omega_3 \geq \cdots \geq \omega_m > 0. \qquad (4.3)$$

Also the eigenfunction $\Phi_1(\vec{x})$ with the largest eigenvalue ω_1 is of one sign for all $\vec{x}$. Furthermore, for each $j = 1, \ldots, m$,

$$\Phi_j(\vec{x}) \sim C_j(\theta)(k_j r)^{-1/2} e^{-k_j r} \qquad \text{when } k_j r \gg 1, \qquad (4.4)$$

for some $C_j(\theta)$. Here

$$k_j = \sqrt{\omega_j/D}, \tag{4.5}$$

and r and θ are defined by $\vec{x} - \vec{x}_0 \equiv r(\cos\theta, \sin\theta)$.

Additionally there is a two dimensional continuum of eigenfunctions $\Phi(\vec{k}, \vec{x})$. These functions have the eigenvalues $-D|\vec{k}|^2$, and are the solutions of

$$\Phi(\vec{k}, \vec{x}) = e^{i\vec{k}\cdot\vec{x}} + \frac{i\Gamma}{4D}\int H_0^{(1)}(|\vec{k}||\vec{x}-\vec{y}|)\alpha(\vec{y})\Phi(\vec{k}, \vec{y})\,dy, \tag{4.6}$$

where $H_0^{(1)}$ is the zero-order outgoing Hankel function. Finally, the continuous eigenfunctions plus the m discrete ones form a complete set over the space of $\mathcal{L}_2$ functions.

We now solve (4.1). First we define $Z(T, \vec{x}) = H(T, \vec{x}) + u(T, \vec{x})$, where $H(T, \vec{x})$ is the solution of

$$H_T = D\nabla^2 H, \qquad H(0, \vec{x}) = Z(0, \vec{x}) = e^{\Gamma\psi(0, \vec{x})}. \tag{4.7}$$

Then u is the solution of

$$u_T = D\nabla^2 u + \Gamma\alpha(\vec{x})u + \Gamma\alpha(\vec{x})H(T, \vec{x}), \qquad u(0, \vec{x}) \equiv 0. \tag{4.8}$$

At each T, $\alpha(\vec{x})H(T, \vec{x})$ is in $\mathcal{L}_2$, so we can solve (4.8) by expanding u and $\alpha(\vec{x})H(T, \vec{x})$ in terms of the eigenfunctions $\Phi_j(\vec{x})$ and $\Phi(\vec{k}, \vec{x})$. This yields

$$\psi(T, \vec{x}) = \Gamma^{-1}\log Z(T, \vec{x}), \tag{4.9}$$

where

$$Z(T, \vec{x}) = \beta_1 e^{\omega_1 T}\Phi_1(\vec{x}) + \sum_{j=2}^{m}\beta_j e^{\omega_j T}\Phi_j(\vec{x}) + H(T, \vec{x})$$

$$- \sum_{j=1}^{m}\gamma_j(T)\Phi_j(\vec{x}) + v(T, \vec{x}). \tag{4.10}$$

Here,

$$\beta_j \equiv \int\Phi_j(\vec{x})e^{\Gamma\psi(0, \vec{x})}\,dx \cdot \left[\int\Phi_j^2(\vec{x})\,dx\right]^{-1},$$

$$\gamma_j(T) \equiv \int\Phi_j(\vec{x})H(T, \vec{x})\,dx \cdot \left[\int\Phi_j^2(\vec{x})\,dx\right]^{-1}, \tag{4.11}$$

and v is the contribution from the continuous spectrum

$$v(T, \vec{x}) \equiv \int \eta(T, \vec{k})\Phi(\vec{k}, \vec{x})\, dk,$$

$$\eta(T, \vec{k}) \equiv \Gamma \int_0^T e^{-Dk^2 s}\left[\int \Phi^*(\vec{k}, \vec{x})\alpha(\vec{x})H(T - s, \vec{x})\, dx\right] ds, \quad (4.12)$$

where * denotes complex conjugate.

Now $\psi(0, \vec{x})$ is bounded, so there are constants C_1 and C_2 such that $0 < C_1 \le H(T, \vec{x}) \le C_2$ for all $\vec{x}$ and all $T \ge 0$. Thus (4.11) shows that each $\gamma_j(T)$ is also bounded. In Appendix I we show that for some constant C_3, $|v(T, \vec{x})| \le C_3 T$ for all $\vec{x}$ and all $T \ge 0$. There we also show that $|v(T, \vec{x})| \ll \beta_1 e^{\omega_1 T}\Phi_1(\vec{x}) + H(T, \vec{x})$ at all $\vec{x}$ when $T \gg 1$. Finally, (4.3)–(4.5) show that each of the first m terms in (4.10) decays exponentially in space, but *grows* exponentially in time, with the first term growing at the fastest rate.

Therefore, in the region where

$$e^{\omega_1 T - k_1|\vec{x} - \vec{x}_0|} \ll 1, \qquad T \gg 1, \quad (4.13)$$

the $H(T, \vec{x})$ term is much larger than all the other terms in (4.10). Using (4.9) and (2.11), we thus find that

$$\mathbf{A}(t, \vec{x}) \approx \mathbf{B}(t + \Gamma^{-1}\log H(T, \vec{x})). \quad (4.14)$$

Moreover, (4.7) shows that $H(T, \vec{x})$ goes to a constant as T becomes large. So we conclude that in the region where (4.13) holds, the system evolves into a spatially constant bulk oscillation.

On the other hand, in the region where

$$e^{\omega_1 T - k_1|\vec{x} - \vec{x}_0|} \gg 1, \quad (4.15)$$

the first term in (4.10) is much larger than all the other terms. Noting that $\beta_1\Phi_1(\vec{x}) > 0$ for all $\vec{x}$, we rewrite (4.9), (4.10) as

$$\psi(T, \vec{x}) = \omega_1 T/\Gamma + \Gamma^{-1}\log\beta_1\Phi_1(\vec{x}) + \Gamma^{-1}E(T, \vec{x}). \quad (4.16)$$

Here the error term $E(T, \vec{x})$ is

$$E(T, \vec{x}) = \log\left\{1 + \left[\sum_{j=2}^m e^{-(\omega_1 - \omega_j)T}\Phi_j(\vec{x})\right.\right.$$

$$\left.\left. + e^{-\omega_1 T}\left(H(T, \vec{x}) - \sum_{j=1}^m \gamma_j(T)\Phi_j(\vec{x}) + v(T, \vec{x})\right)\right]\middle/[\beta_1\Phi_1(\vec{x})]\right\}.$$

$$(4.17)$$

Equations (4.3)–(4.5) show that $E(T, \vec{x}) \ll 1$ when (4.15) is satisfied. They also show that $E(T, \vec{x})$ decays exponentially in T for fixed $\vec{x}$. Together, (4.16) and (2.11) yield our target pattern solution

$$A(t, \vec{x}) = B\left([1 + \epsilon\omega_1/\Gamma]t + \Gamma^{-1}\log\Phi_1(\vec{x}) + \Gamma^{-1}\log b_1\right) + 0(\epsilon),$$

$$(4.18)$$

where we have omitted the small error term $E(T, \vec{x})$.

We now examine the qualitative behavior of the target pattern solution (4.18). First, the bulk oscillation $B(t)$ is periodic with period P, so (4.18) is time-periodic with period $P_t = P/(1 + \epsilon\omega_1/\Gamma)$. Moreover (4.4) shows that when $k_1 |\vec{x} - \vec{x}_0| \equiv k_1 r \gg 1$, (4.18) reduces to

$$A(t, \vec{x}) \equiv B\left([1 + \epsilon\omega_1/\Gamma]t - k_1 r/\Gamma + \Gamma^{-1}\log b_1 C_1(\theta)(k_1 r)^{-1/2}\right)$$

$$(4.19)$$

So when $k_1 r \gg 1$, the target pattern is asymptotic to a cylindrical wave with a radial phase speed

$$v_{ph} = \Gamma(1 + \epsilon\omega_1/\Gamma)/k_1 = \text{sgn}(\Gamma)\sqrt{\epsilon D |\Gamma|}\left|\frac{P}{P_t}\frac{P}{P - P_t}\right|^{1/2}. \quad (4.20)$$

In particular, the target pattern is outgoing if $\Gamma > 0$ and ingoing if $\Gamma < 0$, the opposite of the target patterns in Section 3.

Second, the target pattern solution (4.18) is valid only in the region where (4.15) is satisfied. Since $T = \epsilon t$, the region occupied by the target pattern spreads outward from $\vec{x} = \vec{x}_0$ at the constant radial speed

$$v_{sp} = \epsilon\sqrt{D\omega_1} = \sqrt{\epsilon D |\Gamma|}\left|\frac{P - P_t}{P_t}\right|^{1/2}. \quad (4.21)$$

Recall that the diffusion matrix in (1.1) is ϵD_M. We can make all dependence on ϵ explicit by replacing $\vec{x}$ by $\sqrt{\epsilon}\,\vec{x}_d$. In terms of the new variable $\vec{x}_d$, the diffusion matrix in (1.1) is just D_M and the velocities v_{ph} and v_{sp} in (4.20) and (4.21) are multiplied by $\epsilon^{-1/2}$.

Finally except for the overall phase shift $\Gamma^{-1}\log b_1$, the target pattern (4.18) is independent of the initial conditions $\psi(0, \vec{x})$. It depends only on Γ, on the largest eigenvalue ω_1, and on its eigenfunction $\Phi_1(\vec{x})$. Moreover, $\alpha(\vec{x}) \equiv 0$ except in the area $|\vec{x} - \vec{x}_0| < R$. If R is small, then ω_1 and Φ_1 are

explicitly given by

$$\omega_1 = Dk_1^2,$$

$$k_1 = 2\exp -\left\{\gamma + \frac{2\pi D + \Gamma\int\alpha(\vec{x})\log|\vec{x} - \vec{x}_0|\,dx}{\Gamma\int\alpha(\vec{x})\,dx}\right\} + \cdots, \quad (4.22)$$

$$\Phi_1(\vec{x}) = 2\pi D\Big/\left(\Gamma\int\alpha(\vec{x})\,dx\right) + 0(R^2\log R) \quad \text{for } |\vec{x} - \vec{x}_0| \leq R,$$

$$\Phi_1(\vec{x}) = K_0(k_1|\vec{x} - \vec{x}_0|)\left[1 + 0(R^2\log R)\right] \quad \text{for } |\vec{x} - \vec{x}_0| \geq R,$$

where γ is Euler's constant and K_0 is the zero-order modified Bessel function.

5. INTERACTING TARGET PATTERNS

We now assume that $\alpha(\vec{x}) \equiv 0$ except in the two well-separated regions $|\vec{x} - \vec{x}_1| \leq R_1$ and $|\vec{x} - \vec{x}_2| \leq R_2$. We also assume that $\int_{|\vec{s}| \leq R_i}\Gamma\alpha(\vec{x}_i + \vec{s})\,ds > 0$ for both $i = 1$ and $i = 2$. We solve (2.9) for bounded initial conditions $\psi(0, \vec{x})$, and we find that $\psi(T, \vec{x})$ is given by (4.9)-(4.12) exactly as before. The only change is that some of the discrete eigenfunctions $\Phi_j(\vec{x})$ are centered around $\vec{x} = \vec{x}_1$ and satisfy

$$\Phi_j(\vec{x}) \sim C_j(\theta_1)(k_jr_1)^{-1/2}e^{-k_jr_1} \quad \text{for } r_1 \gg 1, \quad (5.1)$$

where r_1 and θ_1 are defined by $|\vec{x} - \vec{x}_1| \equiv r_1(\cos\theta_1, \sin\theta_1)$. The other discrete eigenfunctions are centered around $\vec{x} = \vec{x}_2$ and satisfy

$$\Phi_j(\vec{x}) \sim C_j(\theta_2)(k_jr_2)^{-1/2}e^{-k_jr_2} \quad \text{for } r_2 \gg 1, \quad (5.2)$$

where $|\vec{x} - \vec{x}_2| \equiv r_2(\cos\theta_2, \sin\theta_2)$. In (5.1) and (5.2), $k_j \equiv \sqrt{\omega_j/D}$ as before.

Let ω_1 be the largest eigenvalue whose eigenfunction $\Phi_1(\vec{x})$ is centered around $\vec{x} = \vec{x}_1$. Similarly, let ω_2 be the largest eigenvalue whose eigenfunction $\Phi_2(\vec{x})$ is centered around $\vec{x} = \vec{x}_2$, and assume that $\omega_1 > \omega_2$. Then in the region where

$$e^{\omega_1 T - k_1|\vec{x} - \vec{x}_1|} \ll 1, \quad e^{\omega_2 T - k_2|\vec{x} - \vec{x}_2|} \ll 1, \quad T \gg 1, \quad (5.3)$$

the $H(T, \vec{x})$ term in (4.10) dominates. Thus, $A(t, \vec{x})$ is given by (4.14) as before. So, in this region the system evolves into a spatially constant bulk oscillation.

In the region where

$$e^{\omega_1 T - k_1 |\vec{x} - \vec{x}_1|} \gg 1, \qquad e^{\omega_2 T - k_2 |\vec{x} - \vec{x}_2|} \ll 1, \tag{5.4}$$

the first term in (4.10) is much larger than all the other terms. So here

$$A(t, \vec{x}) = B([1 + \epsilon\omega_1/\Gamma]t + \Gamma^{-1}\log b_1 \Phi_1(\vec{x})) + 0(\epsilon), \tag{5.5}$$

analogous to (4.18). Additionally, when $k_1 |\vec{x} - \vec{x}_1| \gg 1$, the argument of B in (5.5) reduces to $[1 + \epsilon\omega_1/\Gamma]t - k_1|\vec{x} - \vec{x}_1|/\Gamma + \cdots$. Therefore (5.5) represents a target pattern centered near $\vec{x} = \vec{x}_1$. Similarly, in the region

$$e^{\omega_2 T - k_2 |\vec{x} - \vec{x}_2|} \gg 1, \qquad e^{\omega_1 T - k_1 |\vec{x} - \vec{x}_1|} \ll 1, \tag{5.6}$$

we have

$$A(t, \vec{x}) = B([1 + \epsilon\omega_2/\Gamma]t + \Gamma^{-1}\log b_2 \Phi_2(\vec{x})) + 0(\epsilon), \tag{5.7}$$

which represents a target pattern centered near $\vec{x} = \vec{x}_2$.

Finally, when T is large enough there is an overlap region where

$$e^{\omega_1 T - k_1 |\vec{x} - \vec{x}_1|} \gg 1, \qquad e^{\omega_2 T - k_2 |\vec{x} - \vec{x}_2|} \gg 1. \tag{5.8}$$

For this region we keep the first two terms in (4.10), obtaining

$$A(t, \vec{x}) = B\left(t + \Gamma^{-1}\log\left\{\sum_{j=1}^{2} \beta_j e^{\omega_j T} \Phi_j(\vec{x})\right\}\right) + 0(\epsilon). \tag{5.9}$$

This equation describes how target patterns interact.

At any T and $\vec{x}$ where

$$e^{\omega_1 T - k_1 |\vec{x} - \vec{x}_1|} \gg e^{\omega_2 T - k_2 |\vec{x} - \vec{x}_2|} \gg 1, \tag{5.10}$$

the $j = 1$ term is much larger than the $j = 2$ term in (5.9). Consequently, at this T and $\vec{x}$ we can neglect the latter term, and so (5.9) reduces to (5.5). Thus, at this T the target pattern centered at $\vec{x}_1$ extends to the point $\vec{x}$. Similarly, at any T and $\vec{x}$ where

$$e^{\omega_2 T - k_2 |\vec{x} - \vec{x}_2|} \gg e^{\omega_1 T - k_1 |\vec{x} - \vec{x}_1|} \gg 1, \tag{5.11}$$

(5.9) reduces to (5.7). So, the point $\vec{x}$ is part of the target pattern centered at $\vec{x}_2$ at this T. Since $\omega_1 > \omega_2$ has been assumed, at any point $\vec{x}$ eventually (5.10) will hold. Thus, as T increases the target pattern centered near $\vec{x} = \vec{x}_1$ encroaches upon the other target pattern. Eventually the second target

pattern is engulfed; it will be unobservable when

$$\left(\frac{\omega_1}{k_1} - \frac{\omega_2}{k_2}\right)T - |\vec{x}_1 - \vec{x}_2| \gg 1. \tag{5.12}$$

If $\alpha(\vec{x}) \equiv 0$ except in $n \geq 2$ well-separated areas $|\vec{x} - \vec{x}_i| \leq R_i$, $i = 1, \ldots, n$, an analysis like the preceding one can be done. Around each point $\vec{x}_i$ there is a target pattern with frequency $(1 + \epsilon\omega_i/\Gamma)P^{-1}$ occupying the region where $e^{\omega_i T - k_i|\vec{x} - \vec{x}_i|} \gg 1$. As T increases, the domains of neighboring target patterns will overlap. Then the target patterns with the larger ω's will encroach upon, and eventually engulf, their neighbors. When T is large enough, only the target pattern with the largest ω will remain.

6. Extensions

The analysis in Sections 4 and 5 pertains only to two spatial dimensions. An identical analysis can be used for one spatial dimension. The only change is that the $(k_j r)^{-1/2}$ factors in (4.4), (4.19), (5.1), and (5.2) are absent in one dimension. However, the analysis for three dimensions hinges on whether (4.2) has a discrete eigenpair ω_1, $\Phi_1(\vec{x})$ with $\omega_1 > 0$. If $\Gamma\alpha(\vec{x})$ is large enough over a large enough volume, then such a discrete eigenpair would exist. If such an eigenpair exists, then the analysis and results are virtually identical to the one and two dimensional cases. Otherwise only $H(T, \vec{x})$ and the term analogous to $v(T, \vec{x})$ would be present in (4.10), and no spherical target patterns would develop.

The analysis can also be extended readily to include systems with delayed reaction terms, which often occur in population models. For example, (1.1) can be replaced by

$$\mathbf{A}_t = \mathbf{F}\left(\mathbf{A}, \int_0^\infty G(s, \mathbf{A}(t - s, \vec{x}))\, ds\right) + \epsilon D_M \nabla^2 \mathbf{A}$$

$$+ \epsilon \mathbf{g}\left(\vec{x}, \mathbf{A}, \int_0^\infty K(s, \mathbf{A}(t - s, \vec{x}))\, ds\right). \tag{6.1}$$

If (6.1) has a stable periodic solution $\mathbf{A}(t, \vec{x}) = \mathbf{B}(t) = \mathbf{B}(t + P)$ at $\epsilon = 0$, then we again obtain (2.9)-(2.11), and the analysis proceeds as before.

7. Remarks

We used perturbation techniques to derive (2.9)-(2.11) from (1.1), and then solved (2.9) to obtain target patterns. By using perturbation theory, we have restricted attention to solutions which are near the stable limit cycle $\mathbf{B}$

for all t and $\vec{x}$. There may be other stable solutions of (1.1) which are far from the limit cycle at some $\vec{x}$ for all t [10].

Also, the perturbation scheme we used tacitly assumes that $g(\vec{x}, A)$ varies significantly only on the $O(1)$ and larger length scales. This restriction is unnecessary. If $g(\vec{x}, A)$ varies significantly on very small length scales, a similar perturbation scheme can be employed. This alternative perturbation scheme yields solutions of (1.1) given by (2.9)–(2.11), exactly as before.

Additionally, the length scale in (1.1) has been chosen so that the diffusion term is the same order as the inhomogeneous term $g(\vec{x}, A)$. This was necessary. If we used a shorter length scale, then the diffusion term would dominate the inhomogeneous term. To leading order, we would obtain (2.11) and (2.9) with $\alpha(\vec{x}) \equiv 0$. As shown in Section 3, if $\alpha(\vec{x}) \equiv 0$ and if $\psi(0, \vec{x})$ is bounded, then $\psi(T, \vec{x}) \rightarrow$ constant as T becomes large. That is, after an initial period of time, ψ would become constant (to leading order) on all length scales smaller than the one we have used. On the other hand, if a larger length scale was used, then the $\epsilon g(\vec{x}, A)$ term would dominate the diffusion term. This results in an inconsistent perturbation scheme.

The target pattern solutions obtained in Sections 4–6 depend heavily on the sign of Γ. If $\Gamma > 0$, then the target patterns are outgoing, their frequency is higher than the frequency of the bulk oscillation, higher frequency target patterns engulf lower frequency ones, and higher frequency target patterns have higher wave numbers. If $\Gamma < 0$, the opposite of each of these occurs. From experimental observations it is clear that $\Gamma > 0$ for both the B–Z reaction and the aggregation of *D. discoideum.*

In both the B–Z reaction and in *D. discoideum*, the periodic solutions are relaxation-oscillation type limit cycles. In this type of cycle, the reaction evolves slowly down a quasi-steady branch, it then jumps to a second quasi-steady branch, it evolves slowly up this branch, and then completes the cycle by jumping back to the first branch. As the reaction nears one of the jump points, a very small perturbation can cause the reaction to jump prematurely. So, even very small inhomogeneities $g(\vec{x}, A)$ can give rise to significant frequency shifts $\alpha(\vec{x})$. Thus target patterns may be more prevalent for relaxation-oscillations than for other types of periodic solutions.

Finally, in [12, 14, 15], a phase-diffusion theory was developed. In this theory, target patterns are given by (2.11), where ψ evolves according to

$$\psi_T = D \nabla^2 \psi + \alpha(\vec{x}) \tag{7.1}$$

instead of (2.9). However, in two dimensions the solution of (7.1) is

$$\psi(T, \vec{x}) = H(T, \vec{x}) + (4\pi D)^{-1} \int \alpha(\vec{y}) E_1\left(|\vec{x} - \vec{y}|^2 / 4DT\right) dy, \tag{7.2}$$

where H is the solution of $H_T = D \nabla^2 H$ with $H(0, \vec{x}) = \psi(0, \vec{x})$, and E_1 is the exponential integral. Equation (7.2) predicts that target patterns will *not* engulf each other, that the frequency of a target pattern will essentially be the frequency of the bulk oscillation, that the region occupied by a target pattern grows like $|\vec{x} - \vec{x}_0| \approx 2\sqrt{DT}$, and that the distance between successive rings of a target pattern grows exponentially in $|\vec{x} - \vec{x}_0|$. We conclude that target patterns cannot be explained by phase-diffusion theory.

APPENDIX I

Here we use Theorems 3 and 5 in [18] to estimate the size of $v(T, \vec{x})$, which is defined in (4.12). To do this, we assume that $\alpha(\vec{x})$ has continuous second derivatives and we recall that for some R, $\alpha(\vec{x}) \equiv 0$ for all $|\vec{x} - \vec{x}_0| \geq R$. Also, since $H(T, \vec{x})$ is the solution of a heat equation with smooth bounded initial conditions, we note that there are constants M_0, M_1, and M_2 such that

$$|H(T, \vec{x})| \leq M_0, \qquad |\vec{\nabla} H(T, \vec{x})| \leq M_1,$$

$$|\nabla^2 H(T, \vec{x})| \leq M_2, \qquad \text{for all } |\vec{x} - \vec{x}_0| \leq R, \qquad \text{all } T \geq 0. \quad (A.1)$$

First, we define

$$\sigma(T, \vec{k}) \equiv \int \Phi^*(\vec{k}, \vec{x}) \alpha(\vec{x}) H(T, \vec{x}) \, dx, \qquad (A.2)$$

where * denotes complex conjugate. Then at any T, Bessel's inequality shows that

$$\|v(T, \vec{x})\|_2^2 \leq \Gamma^2 \lim_{N \to \infty} \int_{K(N)} \left| \int_0^T e^{-Dk^2 s} \sigma(T - s, \vec{k}) \, ds \right|^2 dk, \quad (A.3)$$

where $\| \quad \|_2$ is the $\mathcal{L}_2$ norm and $K(N)$ is the domain $1/N \leq |\vec{k}| \leq N$. Using the Cauchy–Schwartz and Bessel inequalities now yields

$$\|v(T, \vec{x})\|_2^2 \leq \Gamma^2 \lim_{N \to \infty} T \int_0^T \left[\int_{K(N)} \sigma(T - s, \vec{k}) \sigma^*(T - s, \vec{k}) \, dk \right] ds$$

$$\leq \Gamma^2 T \int_0^T \|H(s, \vec{x}) \alpha(\vec{x})\|_2^2 \, ds. \qquad (A.4)$$

From (A.1) we now obtain

$$\|v(T, \vec{x})\|_2 < |\Gamma| M_0 \|\alpha(\vec{x})\|_2 T. \qquad (A.5)$$

Since $D\nabla^2[H(T,\vec{x})\alpha(\vec{x})] + \Gamma\alpha^2(\vec{x})H(T,\vec{x})$ is also in $\mathfrak{L}_2$, a sequence of steps like (A.2)–(A.5) shows that

$$\|D\nabla^2 v(T,\vec{x}) + \Gamma\alpha(\vec{x})v(T,\vec{x})\|_2 \le |\Gamma| \Big[M_0 |\Gamma| \|\alpha^2\|_2$$
$$+ D\{ M_0\|\nabla^2\alpha\|_2 + 2M_1\| |\vec{\nabla}\alpha| \|_2 + M_2\|\alpha\|_2 \} \Big] T. \quad (A.6)$$

So there is a constant M_4 such that $\|\nabla^2 v(T,\vec{x})\|_2 < M_4 T$ for all $T \ge 0$. Thus, v and $\nabla^2 v$ are both in $\mathfrak{L}_2$, so a Sobelev-type inequality shows that

$$|v(T,\vec{x})| \le \sqrt{2\pi} \left(\|v(T,\vec{x})\|_2^2 + \|\nabla^2 v(T,\vec{x})\|_2^2 \right)^{1/2}. \quad (A.7)$$

Therefore, there is a constant C such that

$$|v(T,\vec{x})| \le CT \qquad \text{for all } \vec{x} \text{ and all } T \ge 0. \quad (A.8)$$

For our purposes, (A.8) is an adequate estimate for v in the region $|\vec{x}-\vec{x}_0| \le R$. We now obtain sharper estimates for v in the region $|\vec{x}-\vec{x}_0| > R$. By substituting (4.10) into (4.1), we discover that v is the solution of

$$v_T - D\nabla^2 v = \Gamma\alpha(\vec{x})v + \Gamma\alpha(\vec{x})H(T,\vec{x}) - \sum_{j=1}^{m} \sigma_j(T)\Phi_j(\vec{x}), \quad (A.9)$$

$$v(0,\vec{x}) \equiv 0,$$

where

$$\sigma_j(T) \equiv \Gamma\int\Phi_j(\vec{x})\alpha(\vec{x})H(T,\vec{x})\,dx \cdot \left[\int\Phi_j^2(\vec{x})\,dx\right]^{-1}. \quad (A.10)$$

Therefore, we apply the Green's function

$$G(T-s, \vec{x}-\vec{y}) \equiv [4\pi D(T-s)]^{-1}\exp - \left\{ \frac{|\vec{x}-\vec{y}|^2}{4D(T-s)} \right\}, \quad (A.11)$$

to (A.9) and obtain

$$|v(T,\vec{x})| \le |J^0| + |J^1| + \sum_{j=1}^{m} |J_j|, \quad (A.12)$$

where

$$J^0 \equiv \Gamma\int_0^T\int_\Omega G(T-s, \vec{x}-\vec{y})\alpha(\vec{y})v(s,\vec{y})\,dy\,ds, \quad (A.13)$$

$$J^1 \equiv \Gamma\int_0^T\int_\Omega G(T-s, \vec{x}-\vec{y})\alpha(\vec{y})H(s,\vec{y})\,dy\,ds, \quad (A.14)$$

$$J_j = \int_0^T\int G(T-s, \vec{x}-\vec{y})\sigma_j(s)\Phi_j(\vec{y})\,dy\,ds. \quad (A.15)$$

Here Ω is the region $|\vec{x}-\vec{x}_0| \le R$.

Equation (A.8) shows that $|\alpha(\vec{x})v(T, \vec{x})| \leq B_1 T$ for all $T \geq 0$, for some constant B_1. Therefore

$$|J^0| < B_1 |\Gamma| T \int_0^T \int_\Omega G(T - s, \vec{x} - \vec{y}) \, dy \, ds, \qquad \text{(A.16)}$$

$$|J^0| < B_1 |\Gamma| T \frac{R^2}{4D} e^{-q} \log\left(1 + \frac{1}{q}\right), \qquad \text{(A.17)}$$

where $q \equiv (|\vec{x} - \vec{x}_0| - R)^2 / 4DT$. Similarly, $|\alpha(\vec{x})H(T, \vec{x})| \leq B_2$ for all $T \geq 0$, for some constant B_2. So

$$|J^1| < B_2 |\Gamma| \frac{R^2}{4D} e^{-q} \log\left(1 + \frac{1}{q}\right). \qquad \text{(A.18)}$$

Finally, there is some constant N_j such that $|\sigma_j(T)\Phi_j(\vec{x})| \leq N_j e^{-k_j |\vec{x} - \vec{x}_0|}$ for all $\vec{x}$ and all $T > 0$. Thus

$$|J_j| \leq N_j \int_0^T \int G(T - s, \vec{x} - \vec{y}) e^{-k_j |\vec{y} - \vec{x}_0|} \, dy \, ds, \qquad \text{(A.19)}$$

$$|J_j| < \frac{N_j}{2D} \int_0^\infty r e^{-k_j r - (r - |\vec{x} - \vec{x}_0|)^2 / 4DT} \log\left\{1 + 4DT / (r - |\vec{x} - \vec{x}_0|)^2\right\} dr. \qquad \text{(A.20)}$$

From (A.20) we find that

$$|J_j| < 5 N_j T \left[1 + 2\frac{|\vec{x} - \vec{x}_0|}{\sqrt{DT}}\right] e^{-|\vec{x} - \vec{x}_0|^2 / 4DT}, \qquad \text{if } k_j |\vec{x} - \vec{x}_0| \leq 2\omega_j T,$$

$$|J_j| < 5 N_j T \left[1 + 2\frac{|\vec{x} - \vec{x}_0|}{\sqrt{DT}}\right] e^{\omega_j T - k_j |\vec{x} - \vec{x}_0|}, \qquad \text{if } k_j |\vec{x} - \vec{x}_0| \geq 2\omega_j T. \qquad \text{(A.21)}$$

When $|\vec{x} - \vec{x}_0| - R \gg \sqrt{4DT}$, we use (A.12), (A.17), (A.18), and (A.21) to estimate $v(T, \vec{x})$. Otherwise we use (A.8). In particular, we note that there are positive constants Q and C_1 such that

$$\beta_1 e^{\omega_1 T} \Phi_1(\vec{x}) \geq Q[1 + |\vec{x} - \vec{x}_0|]^{-1/2} e^{\omega_1 T - k_1 |\vec{x} - \vec{x}_0|}, \qquad \text{(A.22)}$$

and

$$H(T, \vec{x}) \geq C_1,$$

for all $\vec{x}$ and all $T \geq 0$. Thus $|v(T, \vec{x})| \ll \beta_1 e^{\omega_1 T} \Phi_1(\vec{x}) + H(T, \vec{x})$ when $T \gg 1$.

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